

Pattern of Infection of *Gammarus aequicauda* (Amphipoda) with Metacercariae of *Levinseniella tridigitata* (Trematoda: Microphallidae)

F. THOMAS, T. DE MEEÛS, AND F. RENAUD

Laboratoire de Parasitologie Comparée (URA 698, CNRS), Université Montpellier II, place Eugène Bataillon, 34095 Montpellier cedex 05, France, e-mail: parasito@crit.univ-montp2.fr, demeeus@crit.univ-montp2.fr, and renaud@crit.univ-montp2.fr

ABSTRACT: We investigated the pattern of infection of *Gammarus aequicauda* (Amphipoda) with metacercariae of *Levinseniella tridigitata* (Trematoda: Microphallidae) in a natural lagoon. Prevalence was significantly higher in females than in males, whereas there was no difference between sexes in parasitic intensity. Despite the very large size of *L. tridigitata* metacercariae, the mean abundance increased with host size and in both sexes, suggesting that the accumulation of this parasite has no significant effect on host survival. *Levinseniella tridigitata* is known not to alter its host's behavior. Our results contrast with those obtained with other helminths that alter host behavior in order to favor their transmission to the definitive host.

KEY WORDS: Trematoda, Amphipoda, *Levinseniella tridigitata*, *Gammarus aequicauda*, host survival.

Several advances in ecology have suggested that reduction in host survival caused by parasitism has immediate effects on the population dynamics and the community structure of both parasites and hosts (Crofton, 1971; Price, 1980; Anderson and Gordon, 1982; Freeland, 1983; Scott and Dobson, 1989; Minchella and Scott, 1991; Jaenike et al., 1995). However, we know little about parasite-induced host mortality in the field, mainly because it is often difficult to demonstrate. What we do know comes largely from laboratory observations or anecdotal evidence (Cox, 1989; Barker et al., 1991; Goater and Ward, 1992). Additionally, experimental investigations in the laboratory frequently involve the exposure of individuals to much higher levels of parasitism than those found in the field. Thus, before considering a parasite as an important biotic constraint on a host population, quantitative field measures are necessary.

For many species of parasites, particularly helminths (cestodes, nematodes, trematodes, and acanthocephalans), continuation of the life cycle requires predation on intermediate hosts by the definitive host. Several studies on crustaceans parasitized by helminth larvae reported a disappearance or an absence of heavily infected hosts in the oldest age classes (Seidenberg, 1973; Camp and Huizinga, 1980; Brown and Pascoe, 1989; Thomas et al., 1995a). Such studies concern helminths, the larvae of which may alter the behavior of their intermediate host and thereby enhance their transmission to the definitive host (i.e., "favorization", in the sense of Combes, 1991). For instance, in the crustacean *Gammarus insensibilis*, infective larvae of *Microphallus papillorobustus* (Rankin, 1940) migrate into the brain, provoking aberrant behavior of the amphipod (Helluy, 1983a, b). The parasite transmission to aquatic birds (definitive host) feeding on gammarids is thus favored (Helluy, 1984). In a previous study (Thomas et al., 1995a), this trematode species was reported to severely affect the population dynamics of *G. insensibilis*. On the other hand, the same parasite on *Gammarus aequicauda* encysts in the abdomen, where it affects neither the behavior (Helluy, 1983a, b) nor the population dynamics of this alternative host (Thomas et al., 1995a). In *Gammarus aequicauda* infected with metacercariae of *Levinseniella tridigitata* (Creplin, 1837), such a "suicidal" behavior never occurs either, because cercariae do not migrate to the brain but also encyst in the abdomen where they a priori cannot provoke behavioral alterations (Helluy, 1981). However, metacercarial cysts of *L. tridigitata* are very large (i.e., $450 \times 650 \mu\text{m}$ versus $270 \times 350 \mu\text{m}$ for *M. papillorobustus*; Rebecq, 1964). Thus, fundamental differences in virulence and in size do exist between these two parasite species. The aim of this study, based on data collected in the field, was to analyze the pattern of infection and evaluate the impact of *L. tridigitata* on the population of its intermediate host, *G. aequicauda*.

Materials and Methods

A large sample of *G. aequicauda* ($N = 929$) was collected in a lagoon from Palavas-les-Flots (southern France, $43^{\circ}25'N$, $3^{\circ}35'E$) during spring 1994. Gammarids were randomly sampled in the aquatic vege-

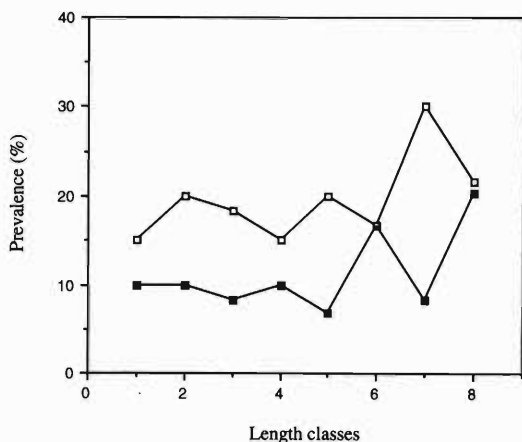


Figure 1. Changes in the prevalence of *Levenseniella tridigitata* with host size in *Gammarus aequicauda* (filled squares: males; open squares: females).

tation. The sampling site was no more than 40 cm in depth. All individuals were immediately preserved in 70% (v ethanol) and were later identified, sexed, measured in length, and dissected in order to count metacercariae of *L. tridigitata* (described in Rebecq, 1964). Following Margolis et al. (1982), we estimated (i) the prevalence (proportion of infected individuals), (ii) the mean parasitic intensity (mean parasite load of infected individuals), and (iii) the mean parasite abundance (total number of parasites divided by the total number of examined hosts). In gammarids, growth conforms to a logistic curve (Sutcliffe et al., 1981), but the relationships between size and age depends largely on temperature, food items, and sex (Sutcliffe et al., 1981). Here, males and females were analyzed separately and arranged in 8 length classes, assuming a positive correlation between age and size. In classes 2 to 7, steps are equal (1 mm for males and 0.5 mm for females). Class 1 includes all individuals that were too small to be in class 2 (i.e., smaller than 11 mm for males and 10 mm for females), and class 8 includes all individuals that were too large to be in class 7. We then analyzed changes in mean parasite abundance with host size.

Statistical tests are described in Siegel and Castellan (1988) and Sokal and Rohlf (1981). All tests are two-tailed. Results were considered significant at the 5% level.

Results

Changes in the prevalence of *L. tridigitata* with host size are presented in Figure 1. Prevalence was significantly higher in females than in males (19.6% for females and 11.3% for males, Fisher's exact test $P = 0.0006$). For the mean intensity, there was no difference between sexes (males, $I = 1.25$; females, $I = 1.32$; Mann-Whitney U -test, $U = 2271$ $P > 0.05$). The frequency distribution of *L. tridigitata* within its host conforms to a negative binomial distribution for males and for

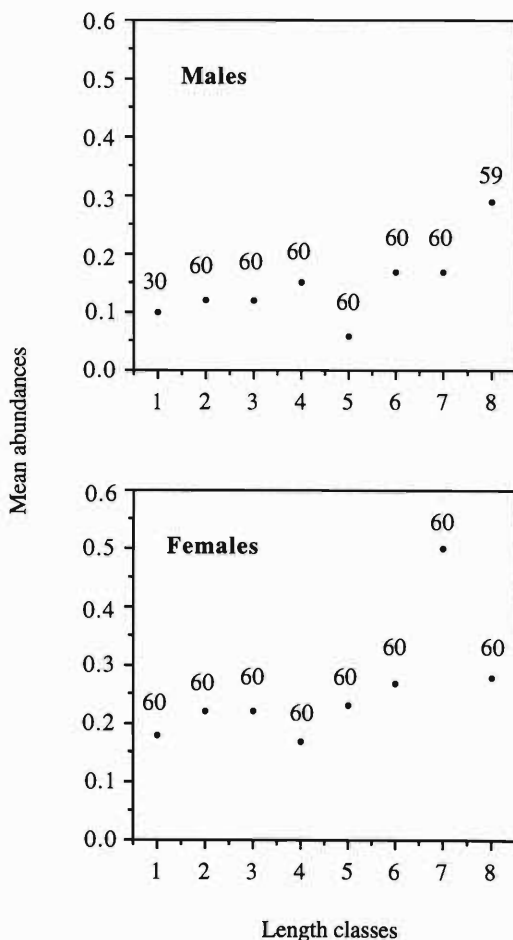


Figure 2. Changes in the mean abundance of *Levenseniella tridigitata* with host size in males and in females of *Gammarus aequicauda*. The number of hosts analyzed in each length class is indicated above each dot.

females (Kolmogorov-Smirnov test, $P > 0.05$ in each case). The values of k (negative binomial parameter) were 0.36 and 0.64 and the means were 0.14 and 0.26 for males and females, respectively. Mean parasite abundance increased steadily with host size in both males ($r_{\text{spearman}} = 0.75$, $P < 0.05$) and females ($r_{\text{spearman}} = 0.83$, $P < 0.05$) (Fig. 2). The maximum mean abundances for males and for females reached 0.29 and 0.5, respectively.

Discussion

The fact that the prevalence was higher in females remains unexplained and contrasts with other studies concerning gammarids infected with

helminths. Indeed, prevalence previously has been reported significantly higher for males for *Gammarus pulex* infected with *Polymorphus minutus* (Ward, 1986) and *G. insensibilis* infected with *M. papillorobustus* (Thomas et al., in press a).

Following Anderson and Gordon (1982), when the rate of host mortality is positively correlated with parasite accumulation, curves of the host age as a function of the parasite abundance are convex, as a consequence of the death of the most heavily infected oldest hosts. However, for parasites of low virulence, continued acquisition through time acts to increase parasite abundance in older classes (Anderson and Gordon, 1982; Gordon and Rau, 1982). To our knowledge, infection with *L. tridigitata* provokes neither behavioral alterations nor color changes of the host (Helluy, 1981). Expectedly, the mean abundance of *L. tridigitata* increased with host size, indicating that, despite the very large size of *L. tridigitata* metacercariae, this parasite has no significant effect, through accumulation, on its host's survival. However, the absence of effect may come from the fact that this parasite does not accumulate enough to significantly affect its host's survival. Indeed, the maximum mean abundance is 4 times lower than what can be observed for *M. papillorobustus* on *G. insensibilis*, where host regulation indeed occurs (Thomas et al., 1995a). Nevertheless, a similar result has already been observed (Thomas et al., unpubl. data) for *G. aequicauda* infected with *Microphallus hoffmanni*, a trematode that also encysts in the abdomen, is unable to provoke behavioral alterations, and significantly accumulates in its host. Literature on parasites that enhance their host's susceptibility to predation by definitive hosts generally lacks quantitative field data. Consequently, the demographic impact of such parasitism on the host population remains mostly unknown. The contrasted pattern of mortality observed between *G. aequicauda* infected with *L. tridigitata*, *M. hoffmanni*, and *M. papillorobustus* and other crustaceans infected by debilitating parasites (Seidenberg, 1973; Camp and Huizinga, 1980; Brown and Pascoe, 1989; Thomas et al., 1995b) suggests that "favorization" has a real impact on the demography of host populations.

In conclusion, this study supports the idea that parasites that cause nonspecific symptoms, as does *L. tridigitata*, may well go unrecognized as

potential regulatory factors, being just "passengers" in their host with little impact on their host's population structure.

Acknowledgments

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1996 Meeting Schedule

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| 14 February 1996 | Nematology Laboratory, USDA, Beltsville, MD (Contact: David Chitwood, 301-504-5660) |
| 20 March 1996 | Johns Hopkins Montgomery County Center, Rockville, MD (Contacts: Thomas Simpson, 410-366-8814 or Alan Scott, 410-955-3442) |
| 4 May 1996 | New Bolton Center, University of Pennsylvania, Kennett Square, PA (Contact: Gerhard Schad, 215-898-6680) |
| October 1996 | Site and date to be announced |
| November 1996 | Site and date to be announced |